Genotype × prenatal and post-weaning nutritional environment interaction in a composite beef cattle breed using reaction norms and a multi-trait model

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ABSTRACT: Environmental effects have been shown to influence several economically important traits in beef cattle. In this study, genotype × nutritional environment interaction has been evaluated in a composite beef cattle breed (50% Red Angus, 25% Charolais, 25% Tarentaise). Four nutritional environments (marginal-restricted [**MARG-RES**], marginal-control [**MARG-CTRL**], adequate-restricted [**ADEQ-RES**], and adequate-control [**ADEQ-CTRL**]) were created based on two levels of winter supplement provided to dams grazing winter range during gestation (MARG and ADEQ) and two levels of input to offspring during post-weaning development (RES and CTRL). Genetic parameters of average daily gain (ADG) during the 140-d post-wean trial, yearling weight (**YW**), and ultrasound measurement of fat depth (**FAT**) at the 12th rib and intramuscular fat percentage (**IMF**) of 3,020 individuals in the four environments were estimated. The heritabilities estimated using a single trait mixed linear model were: ADG: 0.21, 0.23, 0.19 and 0.21; YW: 0.27, 0.33, 0.20 and 0.26; FAT: 0.30, 0.29, 0.29, 0.55; IMF: 0.45, 0.51, 0.33, 0.53 for MARG-RES, ADEQ-RES, MARG-CTRL and ADEQ-CTRL, respectively. The extent of genotype × environment interaction was modeled using two separate methods: reaction norms and multi-trait models. The genetic correlations were estimated using a multi-trait model for ADG, YW, FAT and IMF. Growth traits (ADG, YW) and FAT showed correlations less than 0.80 across the four different environments indicating genotype by environment interaction. For example, genetic correlation for ADG between MARG-CTRL and MARG-RES was 0.65 and 0.73 between ADEQ-RES and MARG-RES. In this example, the former genetic correlation corresponds to differences in post-weaning nutritional environment, and the later represents a nutritional difference imposed on dams (i.e., prenatal environment), potentially mediated via fetal programming. The reaction norm model results were in concordance with the multi-trait model, genotype by environment interaction had a higher effect on traits with a lower heritability.

Key words: environment, fetal programming, genetic correlation, reaction norms

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INTRODUCTION

Economically important traits in beef cattle are under the control of genetic and environmental factors and their interaction. Genotype by environment interaction has been ignored by national cattle evaluation systems, and it is crucial to be taken into consideration in the selection and improvement of beef cattle (De Jong and Bijma, 2002; Huquet et al., 2012). Several studies have shown differences in genetic response and trend across different environments, Williams et al. (2012) observed genetic correlations between weaning weight and post weaning gain measured at low and high altitude lower than 0.8 suggesting genotype by environment interaction and re-ranking in their performance across different altitudes. Moreover, Raidan et al. (2015) observed changes in estimated additive genetic variance and selection to response of average daily gain (ADG) and weaning weight between pasture and feedlot.

Modeling genotype by environment interaction could be implemented using a multi-trait model treating each observation for a given trait in a certain environment as different and assuming potential genetic correlation (Hayes et al., 2003; Mulder and Bijma, 2005; Williams et al., 2012; Raidan et al., 2015). The second approach is using a reaction norm model which requires a continuous environmental descriptor. This approach allows the characterization of the trajectory of animal performance across the environmental gradient (Ravagnolo and Misztal, 2000; Pegolo et al., 2011; Cardoso and Tempelman, 2012; Hammami et al., 2015; Fennewald et al., 2017)

The objective of this study was to evaluate the extent of genotype by nutritional environment interaction on growth and carcass traits in a composite beef cattle breed using a multi-trait and reaction norm model.

MATERIALS AND METHODS

Data

Data used in this study consisted of 3,020 Composite Gene Combination (**CGC**) animals (½ Red Angus, ¼ Charolais, ¼ Tarentaise; Newman et al. 1993a, 1993b) born between 2002 and 2011 at USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT. The Pedigree consisted of 5,371 animals.

Cows were randomly assigned to be fed levels of harvested supplemental feed from December to March of each year that were expected to result in adequate (**ADEQ**; amount of supplemental feed according to industry guidelines) or marginal (**MARG**; ~61% of the supplemental feed provided to ADEQ) levels of protein based on average quality and availability of winter forage. At weaning, daughters from these cows were randomly assigned to either ad libitum (control [**CTRL**]) or restricted (**RES**; 80% of control at a common body weight basis) access to feed for 140-d development post weaning. Similar nutritional treatments were applied to the male offspring, except diet was formulated to provide for greater ADG 0.94 and 0.62 kg ADG for control and restricted, respectively. This design resulted in offspring exposed to one of two prenatal and one of two post-weaning nutritional treatments resulting in four different environments: MARG-CTRL, MARG-RES, ADEQ-CTRL, and ADEQ-RES. Animals used in this study received treatments as described by Roberts et al. (2009).

Phenotypes consisted of ADG during the 140-d post-weaning feeding trial (ADG), yearling weight (**YW**), intramuscular fat percentage (**IMF**) and 12th rib fat depth (**FAT**). Carcass traits were measured using ultra-sound, for further details refer to Roberts et al. (2007). A summary description of the data is presented in Table 1.

Statistical Analyses

Single trait model. A single trait model was implemented in order to estimate variance components of ADG, YW, FAT, IMF phenotypes in each of the four environments. The number of observations was 729, 778, 756, and 757 for MARG-RES,

Table 1. Summary statistics of the dataset for ADG, YW, FAT, and IMF

	ADG, kg/d	YW, kg	FAT, cm	IMF %
MARG-RES				
n	729	729	709	708
Mean	0.52	315.39	0.27	3.00
SD	0.25	71.36	0.10	0.89
ADEQ-RES				
n	764	761	708	708
Mean	0.58	319.27	0.25	3.02
SD	0.24	66.98	0.10	0.91
MARG-CTRL				
n	756	756	756	756
Mean	0.76	355.05	0.35	3.14
SD	0.34	85.43	0.15	0.95
ADEQ-CTRL				
n	757	757	719	719
Mean	0.80	359.82	0.38	3.25
SD	0.32	78.94	0.13	0.89

MARG-CTRL, ADEQ-RES, and ADEQ-CTRL, respectively. The model we used is as follows:

$$y = Xb + Za + e$$

in which **y** is the vector of observations, **X** is the incidence matrix of fixed effects consisting of sex effect, pen and contemporary group effects (year and age-of-dam subclasses), **b** is the vector of solutions of fixed effects, **Z** is the incidence matrix of random additive effects, **a** is the vector of solutions of animal additive effects and **e** is the vector of random residuals. The analysis was carried out using the BLUPF90 package (Misztal et al., 2007).

Multi-trait model. The first model used to evaluate the extent of genotype by environment interaction was a multi-trait model treating each observation of a specific trait in a different environment as a different trait. The four-trait model in matrix notation implemented is the following:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 \\ 0 & 0 & X_3 & 0 \\ 0 & 0 & 0 & X_4 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix}$$
$$+ \begin{bmatrix} Z_1 & 0 & 0 & 0 \\ 0 & Z_2 & 0 & 0 \\ 0 & 0 & Z_3 & 0 \\ 0 & 0 & 0 & Z_4 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix}$$

the terms are similar to the single trait model described above except that in this model each observation for a trait was treated as different. No animal had observations in more than one environment.

The genetic variance covariance matrix **G** was **G** = **G*** ⊗ **A**, where A is the additive relationship matrix and

$$G^* = \begin{bmatrix} \sigma_{11}^2 & \sigma_{12} & \sigma_{13} & \sigma_{14} \\ \sigma_{12} & \sigma_{22}^2 & \sigma_{23} & \sigma_{24} \\ \sigma_{13} & \sigma_{32} & \sigma_{33}^2 & \sigma_{34} \\ \sigma_{14} & \sigma_{42} & \sigma_{43} & \sigma_{44}^2 \end{bmatrix}$$, in which

the diagonal elements are the additive genetic variances for a given trait in each environment, and the off diagonal elements are the genetic co-variances between the different environments. The residual variance matrix is **R** = **R*** ⊗ **I**, where **I** is the identity

matrix and

$$R^* = \begin{bmatrix} \sigma_{e1}^2 & 0 & 0 & 0 \\ 0 & \sigma_{e2}^2 & 0 & 0 \\ 0 & 0 & \sigma_{e3}^2 & 0 \\ 0 & 0 & 0 & \sigma_{e4}^2 \end{bmatrix}$$, in which

$\sigma_{e1}^2, \sigma_{e2}^2, \sigma_{e3}^2$ and σ_{e4}^2 are the residual variances in environments 1, 2, 3 and 4, respectively.

Responses to selection were calculated assuming selection of 20% of individuals, resulting in selection intensity of 1.40. The formula used to calculate direct expected response to selection per generation is the following:

$$\Delta G = i * h^2 * \sigma_p$$

where ΔG is the expected genetic response per generation, i is the selection intensity, h^2 is the heritability and σ_p is the standard deviation of the phenotype.

Indirect correlated expected responses to selection were calculated using the following equation:

$$CR_y = i_x r_{xy} h_x h_y \sigma_{py}$$

in which CR_y is the expected correlated response per generation for a certain trait in environment Y by selecting in environment X, i_x is the selection intensity in environment X, r_{xy} is the genetic correlation for a given trait in environment X and environment Y obtained from the multi-trait model, h_x and h_y are the square root of the heritabilities of a trait in environment X and Y, respectively and σ_{py} is the phenotypic standard deviation in environment Y.

Reaction norms model. The second model used to evaluate genotype by environment interaction was a reaction norm model. In the case of this type of model, the genetic value of the animal is obtained as a function of the average environment which corresponds to the solution of the environmental group the animal record belongs to. In other words, a given animal has a specific genetic value for each environment (Cardoso and Tempelman, 2012). Due to the lack of a continuous environmental co-variable, we adopted a two-step procedure. In the first step, a standard animal model was fit to obtain the genetic value of the animal and the estimates of the effects of the four nutritional environments. The following model was used:

$$y = Xb + Za + e,$$

in which **y** is the vector of observations, **X** is the incidence matrix of fixed effects consisting of sex effect, nutritional environments, pen and contemporary group effects (year and age-of-dam subclasses), **b** is the vector of solutions of fixed effects, **Z** is the incidence matrix of random additive effects, **a** is the vector of solutions of animal additive effects and e is the vector of random residuals.

Then in the second step, a random regression model was fit using the previously estimated nutritional environments as the environmental gradient (Calus et al., 2002; Kolmodin et al., 2002) to express the genetic performance of each animal as a function of the environment gradient in which it was reared. The model in the second step was the following:

$$y_{ij} = x_1^{'}\beta + \varphi \hat{X}_j + a_i + b_i \hat{X}_j + e_{ij},$$

where y_{ij} is the observation of animal i in environment j, β is the vector fixed effects which included pen and contemporary group effects (year and age-of-dam subclasses), φ is the fixed regression coefficient, a_i is the additive genetic value intercept for the reaction norm, b_i is the additive genetic value slope for the reaction norm, $\hat{X}_j$ is the solution of the environment j obtained from the standard animal model in the first step. The

reaction norm model analysis was carried out using the BLUPF90 package (Misztal et al., 2007)

The additive genetic variances were calculated using the following formula:

$$\sigma_a^2 \,|\, env = var(a_i + b_i * env)$$

where a_i is the intercept, b_i is the slope of the reaction norm and env is the environmental co-variable.

The heritability estimates were obtained by:

$$h^2 \,|\, env = \frac{\sigma_a^2 \,|\, env}{\sigma_a^2 \,|\, env + \sigma_e^2}$$

where σ_a^2 is the additive variance, σ_e^2 is the residual variance and env is the environmental gradient.

RESULTS AND DISCUSSION

Variance components using a single trait model in each environment for all traits are presented in Table 2. For ADG, additive genetic and residual variances across the four environments were not greatly different. Heritability estimates ranged from 0.19 to 0.23 which are slightly lower than heritabilities reported in the literature. Crowley et al. (2010)

Table 2. Estimates of variance components for ADG, YW, FAT, and IMF in four different environments using a single-trait animal model

	ADG	YW	FAT	IMF
MARG-RES[a]				
σ_a^2	0.012 (0.004)	1182.46 (383.14)	0.001 (0.0002)	0.108 (0.02)
σ_e^2	0.047 (0.004)	3221.23 (341.80)	0.002 (0.0002)	0.133 (0.02)
h^2	0.21 (0.07)	0.27 (0.07)	0.30 (0.08)	0.45 (0.09)
ADEQ-RES[b]				
σ_a^2	0.014 (0.005)	1261.80 (429.21)	0.0011 (0.0002)	0.136 (0.03)
σ_e^2	0.046 (0.0054)	2538.49 (362.98)	0.002 (0.0002)	0.125 (0.02)
h^2	0.23 (0.09)	0.33 (0.10)	0.30 (0.08)	0.51 (0.11)
MARG-CTRL[c]				
σ_a^2	0.009 (0.004)	904.77 (412.10)	0.0012 (0.0005)	0.091 (0.03)
σ_e^2	0.042 (0.0054)	3533.67 (394.09)	0.002 (0.0002)	0.179 (0.02)
h^2	0.19 (0.07)	0.20 (0.09)	0.29 (0.09)	0.33 (0.11)
ADEQ-CTRL[d]				
σ_a^2	0.012 (0.0045)	1141.02 (402.21)	0.003 (0.0007)	0.139 (0.03)
σ_e^2	0.045 (0.004)	3194.14 (359.88)	0.002 (0.0005)	0.121 (0.02)
h^2	0.21 (0.08)	0.26 (0.08)	0.55 (0.10)	0.53 (0.10)

[a]MARG-RES: Animals fed a restricted amount of feed after weaning and born from dams that were provided marginal levels of winter supplement

[b]ADEQ-RES: Animals fed a restricted amount of feed after weaning and born from dams that were provided adequate levels of winter supplement

[c]MARG-CTRL: Animals fed industry recommended amount of feed after weaning and born from dams that were provided marginal levels of winter supplement

[d]ADEQ-CTRL: Animals fed industry recommended amount of feed after weaning and born from dams that were provided adequate levels of winter supplement

reported a heritability of 0.30 for ADG phenotype in an Irish beef cattle breed and Rolfe et al. (2011) reported a 0.26 heritability in a composite beef cattle breed. Higher estimates for ADG (0.55) were reported in Nellore cattle (Marques et al., 2013). The highest heritability for YW with a value of 0.33 was observed for environment ADEQ-RES and the lowest was observed for MARG-CTRL with heritability of 0.20. The heritability estimates were in concordance with values reported in the literature (Bullock et al., 1993; Moser et al., 1998). For FAT, the highest heritability and highest additive genetic variance was observed in ADEQ-CTRL environment. This high value of additive genetic variance in this environment indicates that genetic expression for FAT was higher. The lowest heritability of 0.29 was observed in MARG-CTRL. For IMF, the highest heritability was also observed in environment ADEQ-CTRL with a value of 0.53 and the lowest was observed in MARG-CTRL environment. Heritabilities were well within the reported estimates in the literature (Crews et al., 2003). The higher the heritability of a trait in a certain environment, the more efficient the genetic response to selection would be (Kearney et al., 2004; Raidan et al., 2015). It is important to note that standard errors of variance component estimates were

relatively high due to the small number of animals in each environment; therefore caution has to be taken in the interpretation of the results.

Expected response to selection per generation was also calculated for all traits in the four environments (Figure 1). Assuming the same selection intensity, For ADG, the expected response to direct selection was slightly higher for animals with adequate feed diet (MARG-CTRL, ADEQ-CTRL). The highest expected response to direct selection for YW was also observed in ADEQ-CTRL and MARG-CTRL. For carcass traits, the highest expected response to direct selection for FAT and IMF was observed in environment ADEQ-CTRL. Moreover, Figure 1 also shows the expected response to indirect selection in different environments. The expected response to indirect selection for ADG was lower than the expected response to direct selection in most environments except for MARG-RES where the response to direct selection was 0.072 kg vs. 0.085 kg for indirect response to selection in ADEQ-CTRL. For YW, the expected response to direct selection was higher than indirect response to selection in all environments. For FAT, expected response to direct selection in environments MARG-RES and ADEQ-RES was smaller than indirect response to selection in ADEQ-CTRL and MARG-CTRL.
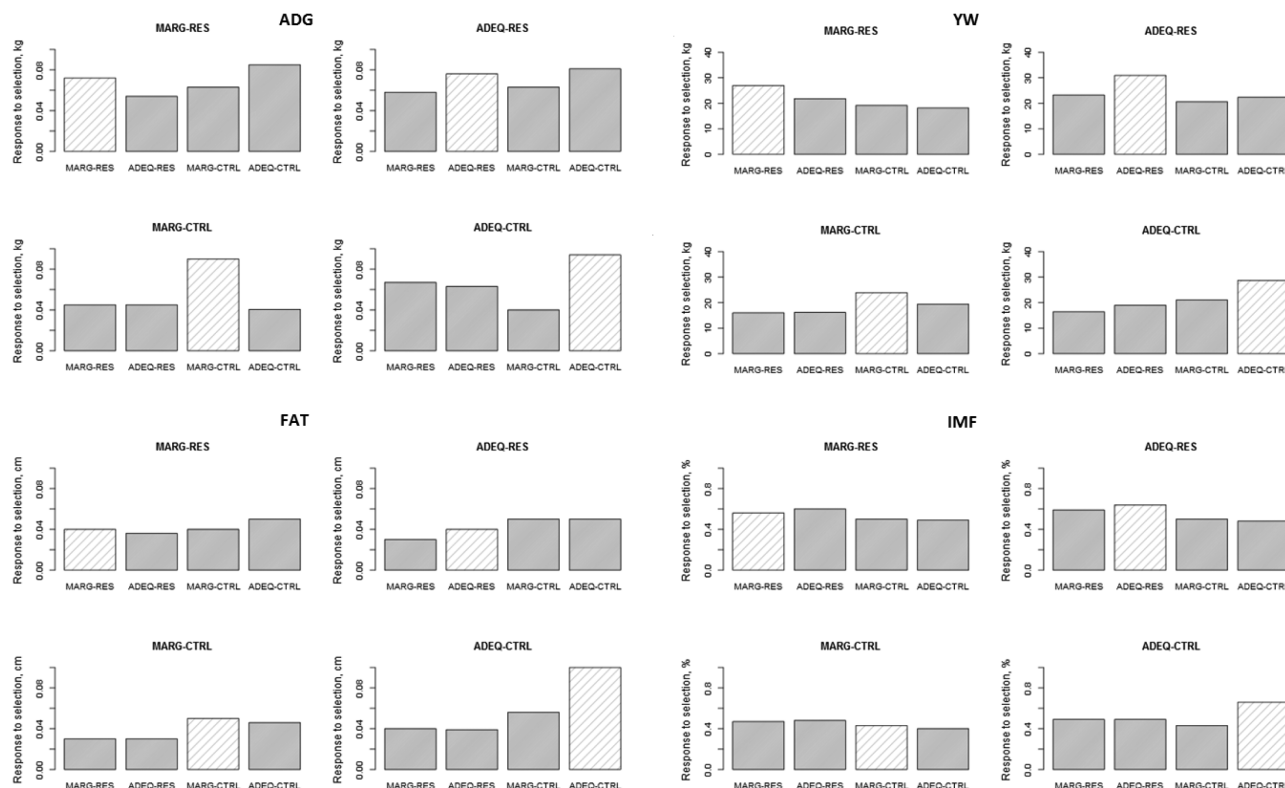
Figure 1. Bar plots of expected response to direct (dashed bars) and indirect selection (solid bars) per generation for ADG, YW, FAT, and IMF in animals from one or four nutritional environments. Animals were born from dams that were provided levels of winter supplement considered to be MARG or ADEQ, and animals were fed either a CTRL or RES amounts of feed after weaning.

Table 3. Genetic correlations for ADG, YW, FAT, and IMF in different environments using a multi-trait animal model

		MARG-RES[a]	ADEQ-RES[b]	MARG-CTRL[c]	ADEQ-CTRL[d]
ADG	MARG-RES	—	0.73 (0.34)	0.65 (0.39)	0.93 (0.11)
	ADEQ-RES		—	0.61 (0.44)	0.82 (0.18)
	MARG-CTRL			—	0.43 (0.28)
	ADEQ-CTRL				—
YW	MARG-RES	—	0.78 (0.12)	0.69 (0.09)	0.62 (0.11)
	ADEQ-RES		—	0.67 (0.15)	0.69 (0.18)
	MARG-CTRL			—	0.77 (0.14)
	ADEQ-CTRL				—
FAT	MARG-RES	—	0.86 (0.16)	0.72 (0.13)	0.70 (0.15)
	ADEQ-RES		—	0.80 (0.15)	0.70 (0.16)
	MARG-CTRL			—	0.66 (0.19)
	ADEQ-CTRL				—
IMF	MARG-RES	—	0.99 (0.10)	0.98 (0.16)	0.81 (0.11)
	ADEQ-RES		—	0.92 (0.13)	0.75 (0.14)
	MARG-CTRL			—	0.78 (0.16)
	ADEQ-CTRL				—

[a]MARG-RES: Animals fed a restricted amount of feed after weaning and born from dams that were provided marginal levels of winter supplement

[b]ADEQ-RES: Animals fed a restricted amount of feed after weaning and born from dams that were provided adequate levels of winter supplement

[c]MARG-CTRL: Animals fed industry recommended amount of feed after weaning and born from dams that were provided marginal levels of winter supplement

[d]ADEQ-CTRL: Animals fed industry recommended amount of feed after weaning and born from dams that were provided adequate levels of winter supplement

Therefore, higher response to selection is achieved in ADEQ-CTRL and MARG-CTRL when selecting for animals in MARG-RES and ADEQ-RES environment. For IMF, higher response to indirect selection was observed in ADEQ-RES than direct response to selection in MARG-RES.

Multi-trait Model

The genetic correlations obtained using a multi-trait model for all traits analyzed are presented in Table 3. Genetic correlations below 0.8 threshold indicate evidence of genotype by environment interaction (Robertson, 1959). From Table 3, ADG was more susceptible to the effect of genotype by environment interaction. The lowest genetic correlation was observed between environment MARG-CTRL and ADEQ-CTRL. This finding is in concordance with the results reported by Raidan et al. (2015) where they found a genetic correlation of 0.49 for ADG between feedlot and pasture using a two-trait model. Mascioli et al. (2006) evaluated genotype by environment interaction effect on ADG from weaning to yearling in beef cattle born in two different seasons (rainy vs. dry) and reported a genetic correlation of 0.8. The genetic correlations of YW in the four environments were also below the 0.8 threshold. However standard errors were

relatively high, as mentioned earlier this could be due to the low number of observations in each of the four environments. Lemos et al. (2015) reported significant genotype by environment interaction in YW using a multi-trait reaction norm model. For FAT, the lowest genetic correlation (0.66) observed was between MARG-CTRL and ADEQ-CTRL. Other environments also showed genetic correlations slightly under the 0.8 threshold. On the other hand, genetic correlations for IMF were above the 0.8 suggesting that genotype by environment effect on this trait was not important.

From the multi-trait model results, it is apparent that the higher the heritability the less impact of genotype by environment interaction on the genetic merit of the animals. Berry et al. (2003), reported significant effect of genotype by environment interaction for lowly heritable traits such as body condition score BCS ($h^2 = 0.08$) and BW change but not significant for milk production which has a moderate heritability of 0.32.

Figure 2 shows the estimated breeding values (**EBV**) of 10 random animals in different environments using the multi-trait model. For ADG, it is apparent that there is evidence of genotype × environment interaction. Ranking of EBV of animals in one environment dropped across different environments. In some instances, management under the
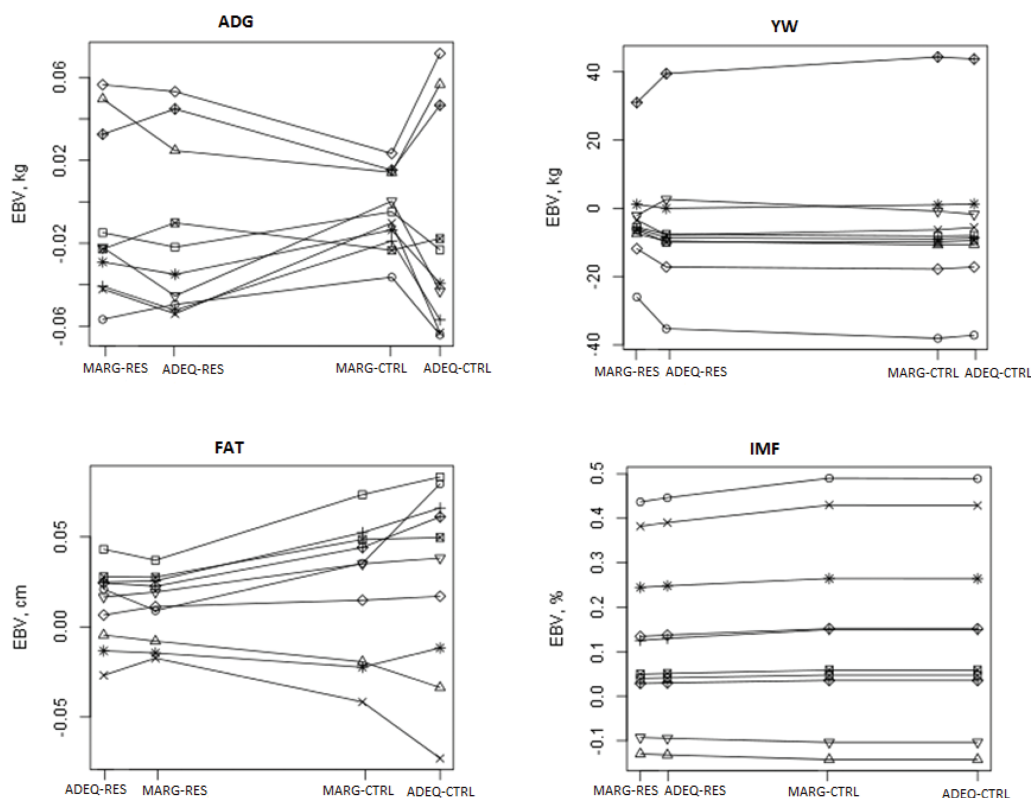
Figure 2. Estimated breeding values for 10 random animals for ADG, YW, FAT, and IMF in different environments using multi-trait model. y-axis is the estimated breeding value and x-axis is the mean in each environment. Animals were born from dams that were provided levels of winter supplement considered to be MARG or ADEQ, and animals were fed either a CTRL or RES amounts of feed after weaning.

Table 4. Estimated variance components of ADG, YW, FAT, and IMF using the reaction norm model

Trait	σ_a^2 [a]	σ_b^2 [b]	σ_e^2 [c]	r_{ab} [d]
ADG	0.099 (0.013)	0.00207 (0.001)	0.32 (0.22)	−0.19 (0.15)
YW	0.063 (0.024)	541.56 (59.08)	1664.0 (927.36)	−0.34 (0.37)
FAT	0.53 (0.16)	0.0005 (0.0002)	0.0072 (0.0035)	0.98 (0.45)
IMF	0.073 (0.028)	0.075 (0.029)	0.13972 (0.09)	0.05 (0.06)

[a]Direct additive genetic variance of the slope

[b]Direct additive genetic variance of the intercept

[c]Residual variance

[d]Correlation between intercept and slope of reaction norm

lowest feed input (MARG-RES) resulted in higher EBV compared to EBV in higher inputs (MARG-CTRL, ADEQ-CTRL). In other words, increasing feed input does not necessarily result in higher EBV. Similar trend was observed for YW and FAT. For IMF, EBVs were relatively constant across environments suggesting a minimal impact of genotype by environment interaction.

Reaction Norms Model

Due to the lack of continuous environmental gradient, estimated fixed effects of the four environments were included as a co-variable and considered as the environmental gradient. Variance components obtained from the reaction norms model are presented in Table 4. The correlations between the intercept and the slope were −0.19, −0.34, 0.98, and 0.05 for ADG, YW, FAT, and IMF, respectively. Higher correlations between intercept and slope indicate that animals with high genetic merit respond better to improvement of the environment (Corrêa et al., 2009; Cardoso et al., 2011). Lower correlations between intercept and slope could potentially mean re-ranking of animals (Pegolo et al., 2011); however looking at reaction norms graph we did not see evidence of re-ranking in IMF which had a correlation of 0.05 (Figure 4).
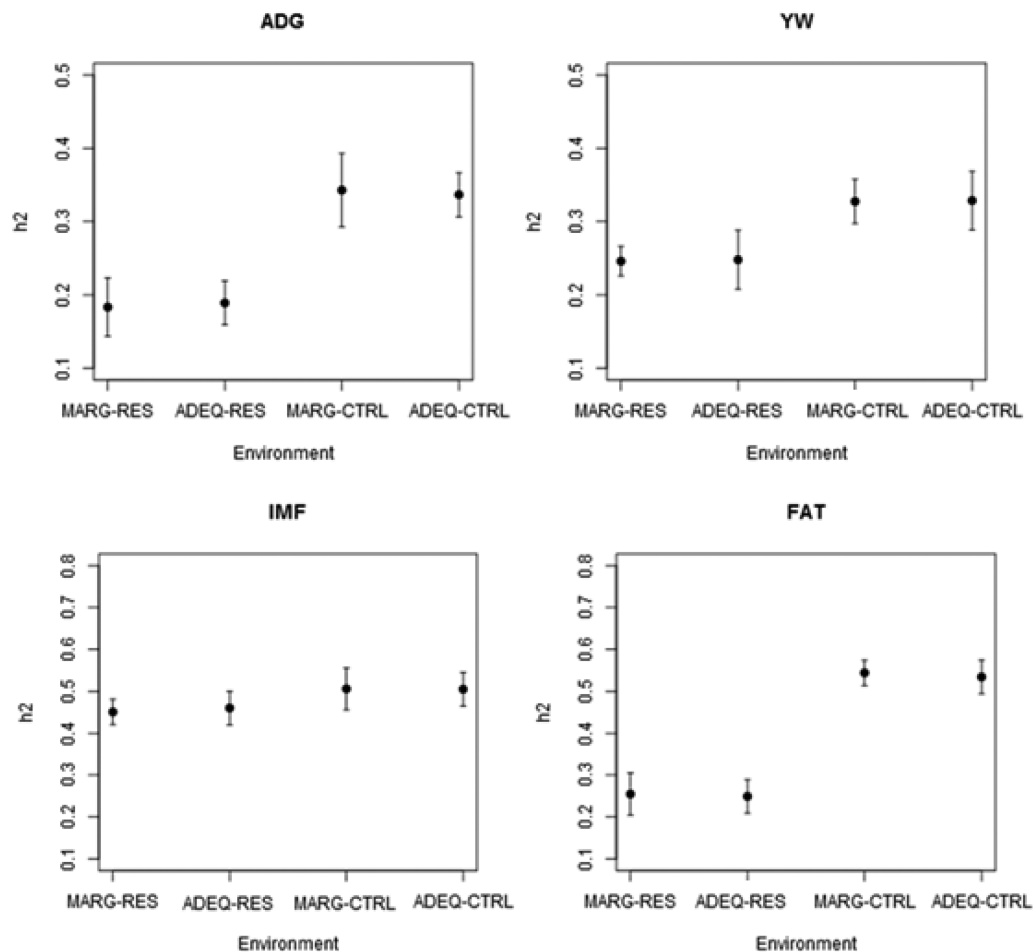
Figure 3. Heritability of ADG, YW, FAT, and IMF in different environments using reaction norm model. Animals were born from dams that were provided levels of winter supplement considered to be MARG or ADEQ, and animals were fed either a CTRL or RES amounts of feed after weaning.

In general, higher heritabilities were observed in higher feed inputs during post weaning period (MARG-CTRL, ADEQ-CTRL) for ADG, YW, and FAT (Figure 3). This trend was more apparent for FAT. On the other hand, no change in heritability estimates was observed for IMF which is in concordance with the multi-trait model results.

The reaction norms of randomly selected animals for each trait were plotted as shown in Figure 4. Patterns indicative of genotype by prenatal environment interaction on ADG, YW and FAT are evident. All three of these traits exhibited greater magnitude of spread between EBVs of animals born from dams provided greater level of winter supplement (ADEQ) than in animals from dams provided less winter supplement (MARG). Reaction norms for IMF did not show an effect of genotype by environment interaction which supports the argument that highly heritable traits are less susceptible to G × E. From the results presented in this study, it is clear that genetically superior animals in a certain environment are not necessarily

superior in another. Furthermore, having higher inputs of feed does not necessarily result in higher genetic response.

Visual comparison of data in Figure 2 (multi-trait model) and Figure 4 (reaction norm model) indicate greater occurrence of re-ranking of EBVs for ADG and YW across prenatal and post-weaning nutritional environments. In contrast, patterns in Figure 4 provide indication of prenatal environmental effects on EBVs, primarily manifested by influence on magnitude in differences among animals, being greater in offspring from dams provided higher levels of winter supplementation. Evidence that level of supplement provided to the dams resulted in fetal programming for phenotypic measurements collected on offspring beyond 1 year of age in these animals has been shown previously (Roberts et al., 2016). Moreover, the observed environmental effect on genetic response could also be due to epigenetics. However, regulation of gene expression is a complex process and techniques such as DNA methylation and histone modifications
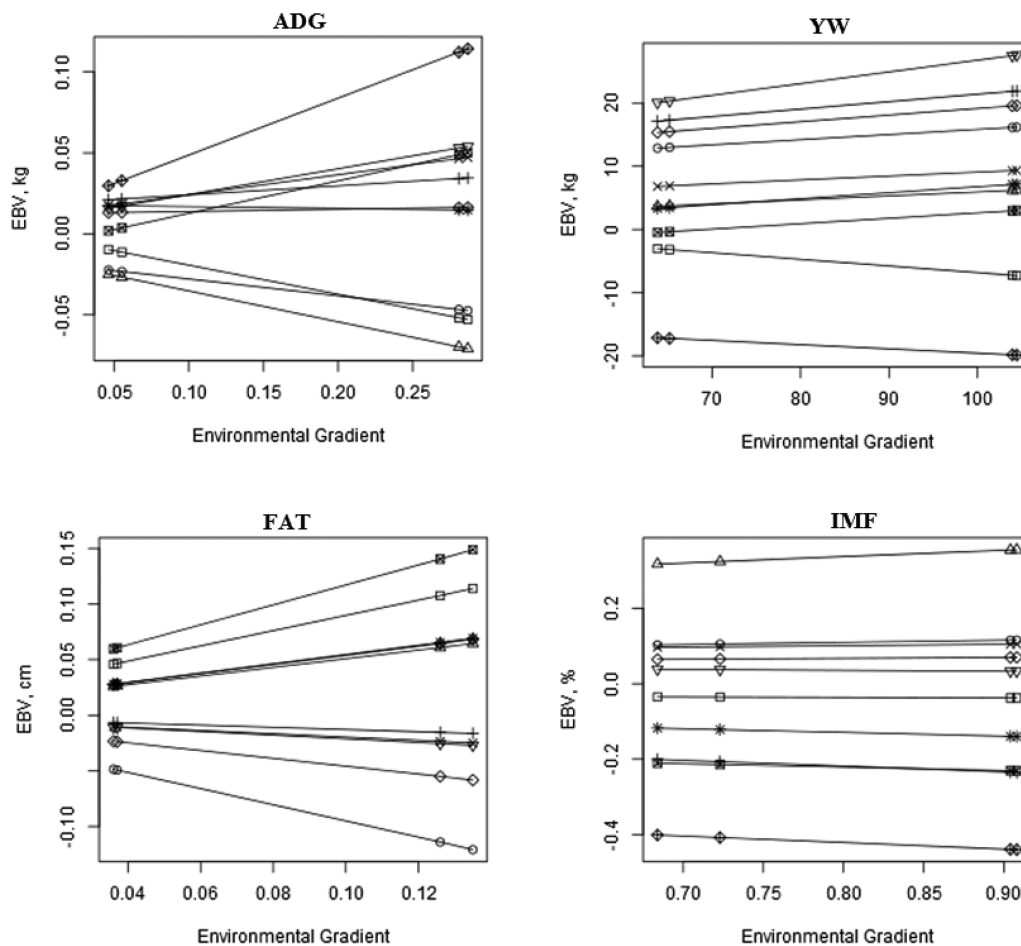
Figure 4. Reaction norms of 10 random animals for ADG, YW, FAT, and IMF using reaction norm model. Animals were born from dams that were provided levels of winter supplement considered to be MARG or ADEQ, and animals were fed either a CTRL or RES amounts of feed after weaning.

processes should be carried out to validate and evaluate the extent of epigenetics impact.

From the present study's results, it is crucial to consider both prenatal and postnatal nutritional environment when developing breeding and selection programs. Mulder et al. (2006) studied genotype by environment impact on several traits in dairy cattle and showed that when having genetic correlations less than 0.8, it is optimal to have production system specific breeding programs. However, in beef cattle most genetic evaluations are based on phenotypic data from a limited range of environments and seldom animals have offspring in very different environments. Genomics could help with this issue, since SNPs could be used to compute genomic breeding values in different environments, however this would require a large reference dataset in each environment.

CONCLUSIONS

All methods applied in the present study demonstrated the existence of genotype by nutritional environment interaction for growth and carcass trait in beef cattle with genetic correlations well below the 0.8 threshold. Further, traits with higher heritability suggest lower susceptibility to the effects of genotype by environment interaction. Furthermore, genetic variation exists in the response of animals to the environment; this key factor could be utilized to select animals that are robust against environmental changes.

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